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THE GENETICS OF POLYMORPHISM IN THE GOOSE *ANSER CAERULESCENS*

F. COOKE AND F. G. COOCH
Dept. of Biology, Queen's University, Kingston, Ontario and Canadian Wildlife Service, Ottawa, Ontario

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Although the most recent A.O.U. check-list of North American Birds (1957) records the Blue Goose and the Lesser Snow Goose as distinct species (*Chen caerulescens* [= *Anser caerulescens*] and *C. hyperborea* [= *A. hyperborea*] respectively), many ornithologists today agree with the conclusion of Cooch (1961) that the smaller subspecies of the Snow Goose *Anser caerulescens caerulescens* is polymorphic and has two clearly defined color phases, a blue phase and a white phase. Some authors, e.g. Manning et al. (1956) prefer to regard the Blue Goose and the Lesser Snow Goose as conspecific but consisting of two subspecies.

Polymorphism is well known in birds and has been well documented by Mayr (1942) and Huxley (1955). In only a few cases, however, has it been possible to infer the genetic basis of the polymorphism. O'Donald and Davis (1959) have studied the genetics of the color phases of the Parasitic Jaeger (*Stercorarius parasiticus*). Meyerriecks (1957) has some observations on genetics of polymorphism in the Great Blue—Great White Heron complex. Williamson (1957) reported on the genetic basis for the dimorphism found in the goslings of the Ross's Goose, and Ryder (1967) extended these observations. Lowther (1961) recorded an interesting case of polymorphism in the White-throated Sparrow and Thorneycroft (1966) presented cytological evidence for the genetic basis of this polymorphism. Most observers, however, have had either to ignore the genetic basis or to suggest a genetic basis with no genetic evidence on which to base their speculations.

Genetic data of this nature are not easy to obtain in non-domesticated birds. Many birds will not breed in captivity. In the wild it is possible to gain meaningful genetic evidence only if a large number of families is studied and if the polymorphism is detectable in nestling stage, or alternatively if the nestling can be kept in captivity, or can be marked for individual recognition until the adult plumage appears. The polymorphism of *Anser caerulescens* is in many ways ideal for study. Large colonies, where the different morphs interbreed, can be found. The polymorphism is detectable in both adult and gosling plumages and is observable in both sexes. Most species of birds produce too few offspring in any one season for a genetic study based on individual families to be feasible, but when a large population can be examined, some pooling of data allows conclusions about the genetic basis to be drawn.

This paper is an attempt to analyze the genetic basis for the polymorphism in this dimorphic species, by investigating a sample of the large colony at Boas River, Southampton Island, North West Territories, Canada. Although there are indications that color differences lead to differences in choice of nest sites and time of breeding, these attributes of the polymorphism have been ignored in the present study. In the course of this analysis, observations on the assortative mating behavior were made. These observations, which are described in detail below, led to the conclusion that some form of imprinting, as suggested by Huxley (1955), was operating. This in turn suggested that such imprinting, if complete, could lead in a few generations

TABLE 1. *Types of progeny produced from the various pairs of geese classified according to plumage.*

Adult plumage classes	Number of pairs	Progeny in plumage class 0	1	2	3	4	Total offspring
0 × 0	254	1041					1041
0 × 1	85	205	16				224
0 × 2	56	154	42				196
0 × 3	9	4	8		16		25
0 × 4	8	6	6		11		23
0 × 5	5	2	4		23		29
0 × 6	4	1	3		4	2	10
0 × 7	3	2	4		4	2	12
1 × 1	27	90	9				99
1 × 2	21	57	33				90
1 × 3	7	3	10		8	5	26
1 × 4	10	9	16		9	3	37
1 × 5	4	3	8		7	4	22
1 × 6	5	3	3		9	3	18
1 × 7	4	2	2		8	4	16
2 × 2	24	20	68	3			91
2 × 3	6		6		12	6	24
2 × 4	5		5		10		15
2 × 5	7		7		28		35
2 × 6	9		6		21	9	36
2 × 7	12	3	6		21	18	48
3 × 3	5	5	5		10		20
3 × 4	4	2	4		16		22
3 × 5	7	2	5		14	4	25
3 × 6	9		1		24	8	33
3 × 7	2	1			6	2	9
4 × 4	11		2		12	20	34
4 × 5	10		2		10	20	32
4 × 6	11		3		11	24	38
4 × 7	13				12	36	48
5 × 5	9		2		9	36	47
5 × 6	11				8	33	41
5 × 7	26				22	90	112
6 × 6	24				21	76	97
6 × 7	23				13	88	101
7 × 7	38					149	149

to separation of the two color morphs into genetically isolated populations and therefore into distinct species. A mathematical formulation of this has recently been presented independently by Seiger (1967) and Kalmus and Maynard Smith (1966). The data presented in this paper support the theories of these authors, and show how valuable a study based on early learning of *Anser caerulescens* could be to an understanding of mechanisms of speciation and polymorphism.

METHOD OF ANALYSIS

Although it has been normal to refer to the morphs as "blue" and "white" (or "snow"), in fact there is more variation in the adult population than these terms would suggest. Some authors have also used the term "heterozygote" to refer to Blue Geese with a considerable amount of white *on the ventral surface*. This term may have been used to imply that the genetic situation was known, but there is no evidence in the literature that these birds are in fact heterozygous. Strictly the term is inaccurate. Nevertheless, the results shown in this paper indicate that such usage is partially correct.

In order to investigate the polymorphism it was first necessary to classify the birds according to the color of their plumage. For this purpose the adults were divided into eight categories defined below.

Class 0.—Body coloration white; tail white; wings with 10 black primaries; white alula, white secondaries and white coverts.

Class 1.—As above but with alula exhibiting varying degrees of darkness; secondaries and coverts white.

Class 2.—As above but with some dark secondaries and frequently streaks of dark in the tertials.

Class 3.—Wings predominantly dark; dark flanks and back; ventral surface white apart from dark coloring around the neck.

Class 4.—As above but with more dark coloring to base of neck; rest of ventral surface white.

Class 5.—As above but with dark ventral surface extending back to fore-sternum.

Class 6.—As above but with dark ventral surface extending back to mid-sternum.

Class 7.—As above but all ventral surface dark apart from occasional small white area around the vent.

Classes 0–2 would generally be considered as Snow Geese. They are white on

TABLE 2. *Comparison between the frequencies of the progeny plumage classes and the adult plumage classes in the total sample.*

Progeny class	0	1	2	3	4	Total
Progeny numbers	1618	286	3	379	642	2928
Progeny frequencies, %	55.3	9.8	0.1	12.9	21.9	100

Adult class	0	1	2	3	4	5	6	7	Total
Adult numbers	381	193	164	54	83	88	120	159	1542
Adult frequencies %	41.2	12.5	10.6	3.5	5.4	5.7	7.8	10.3	100

the body and neck but have varying amounts of dark coloring on the wing.

Classes 3–7 would be considered as Blue Geese. They have varying amounts of white on the ventral surface. The variation is more continuous than the category classification would suggest. Some of the birds in class 3 approach Snow Geese in appearance.

The goslings can be classified according to the color of their down while still in the nest. Five categories could be recognized but the divisions between classes 0 and 1 and between classes 3 and 4 are somewhat arbitrary. The classes of goslings are:

Class 0.—*Golden.* General tone greenish yellow (somewhat grayish on back and wings); medium brownish markings on crown, nape and line of same color through eye; indefinite yellowish patches on back and rump; medium brownish area from thigh to flank; bill light gray with buffy nail; tarsus and feet mostly light gray.

Class 1.—*Dark golden.* Like preceding, except brownish areas on neck and head much darker; line through eye nearly black to jet black (some have blackish eye-ring); general frizzled or near-agouti appearance.

Class 2.—*Dusky.* General tone dusky olive green with overall yellowish wash, but darker (blackish) on head and upper parts; pale yellowish chin patch and narrow yellow line extending up from chin patch to forehead in area immediately behind upper mandible; intense yellow wash on nape of neck and posterior crown; bill and feet mostly sooty black; general color bleaches at a very rapid rate, especially in those areas suffused with yellow wash, and very patchy appearance results within three weeks.

Class 3.—*Dark.* Like 2 except yellowish wash reduced and no yellowish line behind upper mandible; bleaches as preceding, but because wash not initially so intense, bleaching and subsequent contrast not so marked.

Class 4.—*Black.* Except for pale chin-patch, the head, neck, and upperparts dusky brown to sooty black; underparts somewhat lighter (brownish olive); hardly any yellowish wash; bill blackish with whitish nail; hind limbs blackish; the down bleaches uniformly.

In all, 771 nesting pairs were investigated from the Boas River colony. Only those nests where there were two parents were considered. From these pairs, 2928 goslings were classified—an average of 3.82 goslings per breeding pair. From this sample an analysis of the genetic basis of the Blue-Snow polymorphism has been worked out.

RESULTS

All possible mating combinations were found. In all there are 36 such combinations. The progeny from all the crosses within a mating combination (e.g. 0 × 5) have been pooled in respect to offspring color class, and the data are presented in Table 1.

One of the major problems in the analysis is to deduce which gosling plumages correspond to which adult plumages.

TABLE 3. *Comparison between the frequencies of the progeny plumage classes and the adult plumage classes in the total sample. Pooled data.*

	White Morph	Blue Morph
Progeny classes (pooled)	0, 1 and 2	3 and 4
Progeny frequencies	65.2%	34.8%
Adult classes (pooled)	0, 1 and 2	3, 4, 5, 6 and 7
Adult frequencies	67.3%	32.7%

TABLE 4. *Types of offspring obtained from the various crosses. Pooled data.*

Parents	Number of crosses	Number of offspring: White Morph (0-2)	Number of offspring: Blue Morph (3 or 4)
white × white (0-2) (0-2)	170	1741 (100%)	0
white × blue (0-2) (3-7)	98	132 (34.8%)	247
blue × blue (3-7) (3-7)	203	34 (4.2%)	774

It is possible to do this on a statistical basis. It has been calculated by Cooch (1961) that the blue morph in the Boas River population is increasing at the rate of from 1 to 2% per annum. Therefore, the frequency of any one gosling plumage class should not be significantly more than the frequency of a corresponding adult plumage class, if the plumage classifications are genetically determined. For instance, if goslings of plumage class 0 all grow up to be adults of class 0, then the frequency of class 0 goslings in the offspring population would be within a few per cent of the frequency of the class 0 adults in the adult population. By making this comparison one gains an indication of which offspring plumages correspond to which adult plumages. Table 2 shows that there is no good comparison, but if one pools the frequencies of certain of the crosses a good comparison can be made. A number of pooled combinations are possible. The one shown in Table 3 is considered the most probable, firstly because it is statistically the closest and secondly because other interpretations are unrealistic when the data are considered in detail. This comparison of the progeny plumage classes with the adult plumage classes would lead to the conclusion that progeny classes 0, 1 and 2 are young stages of the white morph and classes 3 and 4 are the young stages of the blue morph and the so-called heterozygotes. One cannot rule out the possibility that some class 3 and 4 goslings are white morph and an equal number of class 0, 1 and 2 goslings are blue but genetic evidence gives no indication of this. Where observations have been made on banded goslings retrapped later, the conclusions presented above seem to be valid, with one exception. These are goslings of progeny class 2 which are rare and abnormal in that they give rise to an adult which has essentially a blue goose wing coloration and a snow goose body apart from a small amount of dark coloration on the back of the neck. Such adults have been classified as belonging to adult class 3, which is a blue morph class although the goslings have been assigned to a white morph class. Clearly this is an anomaly and it is felt that the adults should more properly have been placed in class 2. Reasons for this are given later.

With these pooled data, it is possible to simplify the data in Table 1. This simplification is shown in Table 4. These data now fit in well with the hypothesis that the different morphs are due to single allelic differences such that the dominant allele B confers the blue coloration to the goose while the recessive allele b, if homozygous, confers the white coloration. Birds showing the blue morph, therefore, would have the genotypes BB or Bb, while birds showing the white morph would have the genotype bb.

On this hypothesis, if both parents are white (classes 0-2) then all the offspring should be white (offspring class 0, 1 or 2). This was found to be true for all 470 white × white crosses. The outcome of a cross between a white bird and a blue bird would depend upon whether the blue was heterozygous or homozygous. If heterozygous, blue and white offspring would be produced in a 1 : 1 ratio. If homozygous, only blue offspring would be found. The frequency of white offspring from a large mixed sample of crosses would therefore be between 0% and 50%, dependent upon the frequency of homozygotes to heterozygotes in the blue population. The observed frequency was 34.8%. In the blue × blue crosses, white offspring would be produced only if both parents were heterozygous. If all the blue × blue crosses were between heterozygous birds then 25% of the offspring would be white. Clearly some of these crosses involve homozygous birds therefore the frequency of white offspring from a mixed sample of blue × blue crosses would be between 0% and 25%. The observed value is 4.2%. Since assortative mating occurs in the population it is not possible to use a Hardy-Weinberg calculation to estimate the relative frequency of homozygous to heterozygous blue birds.

The results obtained, therefore, are consistent with this simple genetic interpretation. Two problems remain however. Firstly, is the heterozygote morphologically distinct from the homozygous blue? Secondly, what is the explanation for the variation observed within any particular genotype class? These questions are considered below.

TABLE 5. *Proportion of white:blue progeny in crosses where one parent is white (class 0, 1 or 2) and the other parent blue. The 1:1 ratio would be expected if all the blue birds in that class were heterozygous. A P value of less than 5% means that it is unlikely that all the blue birds within that class are heterozygous.*

Adult Plumage Class of Blue Parent	Number of Crosses	Offspring		χ^2 Value, Deviation from 1:1 Ratio	P
		White	Blue		
3	22	31	47	3.3	0.05-0.10
4	23	41	33	0.9	0.30-0.50
5	16	24	62	16.8	<.001
6	18	16	48	16.0	<.001
7	19	19	57	19.0	<.001

Heterogyzotes

Earlier writers have referred to the white-bellied blue birds as heterozygotes. This appellation is only partly borne out by the data. The blue adults were subdivided into classes 3 through 7 on the basis of degree of whiteness on the ventral surface. Although divided into five classes for convenience, the variation between class 3 and class 7 is in fact continuous. The data suggest that most, if not all, of the class 3 birds are heterozygous, and the frequency of heterozygotes in each class diminishes as the degree of whiteness on the ventral surface decreases. Nevertheless, even some class 7 birds (wholly dark belly) must be heterozygous. Heterozygosity of a blue bird is detectable by the ability of that bird to produce a white offspring when mated to either a white bird or another heterozygote. The frequency of white offspring gives a measure (albeit an imprecise measure) of the frequency of heterozygotes.

The frequency can be seen in Tables 5 and 6. Table 5 shows the frequency of white offspring produced when classes 3, 4, 5, 6, and 7, considered separately, are mated with white birds. Table 6 shows the frequency of white offspring produced when classes 3, 4, 5, 6 and 7 are mated with blue birds.

From Table 5 one can deduce that there is no reason to doubt that all class 3 and class 4 are heterozygous, since the frequency of white to blue offspring does not significantly differ from a 1 : 1 ratio, which would be predicted if all these crosses were genetically Bb × bb. Classes 5, 6, and 7 presumably include both homozygous and heterozygous birds. The frequency of white to blue offspring does not fit a 1 : 1 ratio, but neither are all the offspring blue. By looking at the offspring from individual crosses the best estimate for the class 5 birds is that 38%

TABLE 6. *Proportion of white to blue progeny in crosses where both parents are blue.*

Adult Plumage Class of one Blue Parent	Number of Crosses	Offspring		Per Cent White	Estimated† Frequency of Doubly Heterozygous Crosses
		White	Blue		
3*	32	35	94	27.1	100%
4	60	15	193	7.2	28.8%
5	72	13	291	4.2	16.8%
6	102	4	403	1.0	4.0%
7	140	1	567	0.2	0.8%

* The data are pooled such that in class 3, crosses 3 × 3, 3 × 4, 3 × 5, 3 × 6 and 3 × 7 are included. The 3 × 3 group are counted twice, once since bird A of the pair is a class 3 bird mated to a blue bird and once since bird B of the pair is a class 3 bird mated to a blue bird. The same reasoning applies for each class.

† Since 25% of the offspring from a doubly heterozygous cross will be white the frequency of such crosses is 4 × the percentage of white progeny.

are homozygous and 62% heterozygous; for class 6 birds 50% are homozygous and 50% are heterozygous; for class 7 birds 50% are homozygous and 50% are heterozygous. *Table 8 gives details of these* crosses. To calculate the frequencies of heterozygotes to homozygotes an estimate is obtained by observing the frequency of white offspring in the total sample from any particular blue parental class mated to a white bird. Since heterozygotes crossed to white birds give an equal number of white and blue offspring, twice the number of white offspring gives an estimate of the total number of offspring produced by Bb × bb crosses.

If W = number of white offspring from a particular blue × white mating class,

T = total number of offspring from a particular blue × white mating class,

P = frequency of heterozygotes among the blue parental class,

Then $P = 2W/T$ gives the best estimate of this frequency. The P values are tabulated in Table 8.

TABLE 7. *Percentage of white progeny produced when blue birds are mated with birds of the same plumage class. If all birds within the particular class were heterozygotes then around 25% white offspring would be expected.*

Cross (Adult Plumage Classes)	Number of Crosses	White	Blue	Per Cent White Progeny
3 × 3	5	10	10	50
4 × 4	11	2	32	6.2
5 × 5	9	2	45	4.4
6 × 6	24	0	98	0
7 × 7	38	0	149	0

A general conclusion which can be derived from Table 5 and which is consistent with the data, is that all the class 3 and class 4 blue birds which are mated with white birds are heterozygous, and roughly two-thirds of the class 5 and one-half of the class 6 and 7 blue birds which are mated with white birds are heterozygous, the remainder being homozygous. This is summarized in Table 8.

The blue × blue crosses are more difficult to analyze. Only if both parents are *heterozygous is a white offspring possible.* Even if both parents are heterozygous and produce n offspring the chance of all blue offspring is $(0.75)^n$. If a heterozygous pair produce four offspring, there is a 31.6% chance that all will be blue. Nevertheless, if a white offspring is produced it means that both parents were heterozygous. One can see from Table 6 that heterozygosity is not distributed randomly among the five classes, but is frequent among the white bellied birds and rare (but not absent) among the dark bellied birds.

An alternative way of assessing the frequency of heterozygotes among the different classes of blue birds is to consider only those birds which are mated to another of the same class. These data are presented in Table 7. If all blue birds within a class were heterozygous then one would expect 25% of the progeny to be white. The 3 × 3 crosses appear to give a significantly higher frequency than this and this result requires an explanation. It has already been mentioned that the class 2 progeny are white birds since they are produced from two white parents and yet they grow into an abnormal plumage which in this survey has been classified as adult plumage class 3. It seems that in terms of our hypothesis such a bird is genetically bb homozygous recessive. Very few of the class 3 adults are of this genotype since birds of this plumage are rare, but if one or two of the parents in the 3 × 3 crosses are in fact homozygous recessive then this could result in the significant increase of white progeny in this class.

The 4 × 4 crosses and the 5 × 5 crosses suggest that some of each of these classes are homozygous blue and some are heterozygous. The 6 × 6 crosses and the 7 × 7 crosses give no indication of any heterozygotes. Nevertheless, they are relatively small samples and we have already seen that at least a few of the 6 and 7 class birds are heterozygous.

An attempt has also been made to estimate the frequencies of heterozygotes among the different adult plumage classes, as determined by the blue × blue crosses. The frequency of white offspring from blue × blue crosses involving a particular blue parental class gives an estimate of the frequency of heterozygotes in that parental class. When two heterozygotes are mated, 25% of the offspring would be expected to be white; thus 4 × the number of white offspring in the sample gives an estimate of the frequency of Bb × Bb crosses. If one assumes that mating is random between the different genotypes of blue birds then the frequency of heterozygotes in any one class of parents is the square root of the frequency of doubly heterozygous crosses. Thus, following the notation given above: $P = \sqrt{4W/T}$. The assumption of random mating between the genotypes is unlikely to be true since assortative mating has been shown and therefore this method is likely to overestimate the frequency of heterozygotes. From these calculations one can see that class 3 birds are heterozygotes, though

TABLE 8. Calculated frequencies of the different genotypes within the different adult plumage classes, 3-7.

Adult Plumage Class (Blue)	Blue × White Crosses $P = 2W/T$ (see text)	Blue × Blue Crosses $P = \sqrt{4W/T}$ (see text)
3	all Bb	all Bb (few misclassified bb)
4	all Bb	54% Bb, 46% BB
5	62% Bb, 38% BB	41% Bb, 59% BB
6	50% Bb, 50% BB	20% Bb, 80% BB
7	50% Bb, 50% BB	9% Bb, 91% BB

there is some evidence that a few white bb birds have been misclassified. Class 4 and 5 birds consist of heterozygous and homozygous blues. Class 6 and 7 birds consist predominantly of homozygous blues and the frequency of heterozygotes is unlikely to exceed 20%.

It will readily be seen that the frequency of heterozygotes among the blue adult color classes as deduced from the blue × blue crosses is not the same as that calculated from the blue × white crosses. These differences are shown in Table 8. One interesting point emerges from this table. The frequency of heterozygous blue birds which are mated to white birds is considerably higher than the frequency of heterozygotes mated to blue birds. This is certainly true for class 4, 6 and 7 birds and is probably true for class 5. There is no evidence that any of the class 3 birds have the genotype BB. This tendency of heterozygotes to mate with white birds is biologically important and will be discussed later.

A genetic classification of *Anser caerulescens* in terms of this major gene for color under the scheme proposed above would be:

bb—adult classes 0–2 (rarely 3), progeny classes 0–2.

Bb—adult classes 3–7, progeny classes 3 and 4.

BB—adult classes 4–7, progeny classes 3 and 4.

TABLE 9. *Variation of progeny classes produced from crosses between white birds of different adult color classes.*

Class of Mating (Adult color Classes)	Number of Crosses	Progeny Classes		
		0	1	2
0 × 0	254	1041		
0 × 1	88	208	16	
0 × 2	56	154	42	
1 × 1	27	90	9	
1 × 2	21	57	23	
2 × 2	24	20	68	3

This analysis of the Blue Geese strongly suggests therefore that the B allele is incompletely dominant and that there is considerable variability of expression in both homozygous and heterozygous birds.

TABLE 10. *Assortative mating among a) white geese and b) blue geese. The tendency for a bird to be mated with another in the same adult plumage class is noticeable.*

a) White Crosses	Observed	Expected (Assuming Random Mating)	
0 × 0	254	226.1	Total Crosses 470
0 × 1	88	113.0	$\chi^2_5 = 61.35$
0 × 2	56	86.7	
1 × 1	27	14.1	
1 × 2	21	21.6	$P < .001$
2 × 2	24	8.3	

b) Blue Crosses	Observed	Expected (Assuming Random Mating)	
3 × 3	5	1.3	
3 × 4	4	4.7	Total Crosses 203
3 × 5	7	5.7	
3 × 6	9	8.0	
3 × 7	2	11.0	
4 × 4	11	4.4	
4 × 5	10	10.6	$\chi^2_9 = 44.06$
4 × 6	11	15.1	
4 × 7	15	20.7	$P < .001$
5 × 5	9	6.4	
5 × 6	11	18.1	(For the purposes
5 × 7	26	24.8	of the χ^2 test
6 × 6	24	12.8	classes 3 and 4
6 × 7	23	35.2	were lumped since
7 × 7	38	24.1	some expected
			values are low.)

Variation Within the Major Genetic Divisions

Clearly the genetic model presented above does not account for all the plumage variation found in either the adults or the offspring. Homozygous recessive bb birds vary in the amount of dark plumage on the wing. Bb and BB birds vary in the amount of white on the ventral surface. This variation may be environmental, genetic or both. There is evidence that both genetic and non-genetic variations occur. The data have been analyzed only for the white birds, since the difficulty of knowing precisely whether any particular blue bird is homozygous or heterozygous confuses the analysis.

White birds of adult plumage class 2 when mated together may give rise to progeny of class 0, 1 or 2. It was pointed out by Cooch (1961) that if both birds of a pair were of class 2 and if they laid five eggs, the last egg would hatch into a gosling of progeny class 2. Furthermore, the earliest eggs to hatch usually gave progeny class 0 goslings. This variation is probably non-genetic. Degree of offspring coloring is clearly correlated with the length of time between fertilization and hatching. If the variation were genetic, it would be necessary to postulate that certain genotypes were invariably later in hatching than others. Further experimental evidence is needed on this point.

Some of the variation between the white birds does seem to be genetic. The greater the dark coloring on the wing of the parents the greater the proportion of progeny classes 1 and 2 in the offspring. This can be seen in Table 9.

These results suggest that the strain possesses modifier genes which lead to variation in the amount of darkness in the goslings and in the adult wings in bb birds. Perhaps these modifiers also affect the expression of the dominant allele. The hypothesis of a single major gene difference with the B allele incompletely dominant over the recessive allele b, superimposed upon which are modifier genes and some non-genetic variation, is then consistent with the results which are presented in this paper. Other hypotheses tested have proved inadequate to explain the data, or are more complex than the one presented. Whether it is in fact the correct hypothesis will perhaps only be known when controlled matings are carried out with birds in captivity.

Assortative Mating

Cooch and Beardmore (1959) have already recorded assortative mating in the Blue-Snow Goose complex. They showed that birds of similar morph mate with one another more frequently than with birds of the opposite morph. They showed further that when only blue × white crosses were examined, pairs where the white bird was the female significantly outnumber those in which the blue bird was female. This is in contradiction to the observations of Sutton (pers. comm.) who has found that blue females predominate in mixed crosses.

Assortative mating of a more restricted kind can also be demonstrated. Even within the classes based on adult plumage, there is a significantly higher number of pairs in which both birds belong to the same plumage class. This can be seen in Table 10 which shows this effect among white birds and among blue birds. There is another type of assortative mating which affects those blue birds which have mated with white birds. The blue birds with more white in their plumage show a greater tendency to mate with white birds than do those with the darker plumages. This is demonstrated in Table 11.

It was shown in Table 8 that the more white in the Blue Goose plumage, the more likely it is that the bird is heterozygous. A class 3 bird is more likely to be a heterozygote than is a class 7 bird. One can conclude from Table 11 therefore that heterozygous birds mate more frequently with white birds than do homozygous birds.

TABLE 11. *Total frequency of blue birds in each of the five adult plumage classes compared with the frequency with which blue birds in each class are mated to white birds.*

Class of Blue Bird	Number in Class	Number in Class Mated to White Bird	Per Cent of Class Mated to White Bird
3	54	22	40.7
4	83	23	27.7
5	88	16	18.2
6	120	18	15.0
7	159	19	11.9

A further and more cryptic type of assortative mating is also detectable in these data. In adult plumage classes 4, 5, 6 and 7 within a particular class one has both homozygous and heterozygous birds. The heterozygous birds within a class show a greater tendency to mate with white birds than do the homozygous birds. This has been noted earlier and evidence is shown in Table 8.

DISCUSSION

A discussion of the genetic interpretation of the data has already been presented. The data are consistent with the theory that a major pair of alleles controls this avian example of genetic polymorphism. The data are not unequivocal since it appears that there are additional factors such as modifier genes, incomplete dominance and assortative mating. A detailed examination of the assortative mating leads to some interesting theories concerning mate selection in *Anser caerulescens.*

Since all the data presented here come from the same colony, the evidence of assortative mating suggests a selection of particular kinds of mates in this polymorphic population. It is known that the male plays the dominant role in pair formation. If selection is carried out on the basis of plumage color then a simple hypothesis would be to assume that male tends to select a mate with a plumage similar to his own. This agrees with the observations shown on Table 10, but does not explain the observations of Cooch and Beardmore (1959) and Sutton (pers. comm.) in which the two reciprocal types of mixed mating are not equally frequent. Moreover it does not explain why the heterozygous birds within a class show a greater tendency to mate with white birds than do the homozygous birds.

An alternative theory based on imprinting can explain all the data presented in this paper. This theory is that males select a mate with a plumage similar to that of one or both of their parents. Some imprinting mechanism was suggested by Cooch (1963) to explain the fact that the first Blue Geese to appear in previously pure Snow Goose colonies are almost always white-bellied birds, which were assumed to be heterozygotes.

Class 7 birds were shown to be usually *homozygous*, but of the class 7 birds with white mates about 50% were heterozygous. The heterozygous and homozygous class 7 birds do not differ in range of plumage, at least not to the human eye, and yet the heterozygotes are preferentially selecting white mates. The homozygous class 7 birds must have had both parents with blue plumage, whereas the heterozygous birds could have had a white parent. If geese select mates similar to one of their parents then it is expected that heterozygous birds will be more frequent among the blue × white crosses. This theory provides an explanation for the data in Table 8 and 11.

It also provides an explanation for the hitherto unexplained observation that among mixed pairs, the number of blue males mated with white females significantly exceeds the number of white males mated with blue females in the Boas River colony. Assuming that the male plays the dominant role in mate selection, and that the female is passive, then the excess of blue males crossed with white females would suggest that the number of blue males with a white parent exceeds the number of white males with a blue parent in this colony if our theory is correct. From the data in Table 1 it is possible to find out how many of each of these two classes are present. In fact in the sample 8.3% of the white goslings had a blue parent whereas 24.4% of the blue goslings had a white parent. Only 50% of these goslings will be males and will therefore actively select mates, but nevertheless these findings agree precisely with the prediction based on this theory of imprinting.

All the examples of assortative mating presented in this paper can be explained on the basis of the theory that male geese select mates which resemble one of their parents. This theory can be tested in a number of ways. Firstly, families of geese could be studied from one generation to the next to see how precisely this theory holds for particular marked birds. The data presented above are based on a large number of families in a single generation and no attempt has been made to examine the mates of the goslings in this sample in subsequent years. An experiment of this nature should be carried out in the field since experiments with captive birds may result in exceptional mate selections. Secondly, in the white × blue crosses the ratio of blue males and white females to white males and blue females in a population would be dependent upon the overall ratio of blue to white birds in the population if our theory is correct. For example, in this Boas River population the frequency of blue goslings with a white parent exceeds that of white goslings with a blue parent and therefore according to our theory blue males with white females predominate among the mixed crosses. In a population such as the Bowman Bay colony, blue geese are much more common than white geese. In such a colony we would expect white goslings with a blue parent to outnumber blue goslings with a white parent and therefore in the mixed crosses white males and blue females would predominate. It would also be interesting to compare the assortative mating patterns in the South American goose, *Chlorphaga picta*, in which only the male is polymorphic.

The information presented in this paper points to the importance of imprinting as a mechanism for assortative mating and the maintenance of polymorphism in a population. *Anser caerulescens*, therefore, illustrates many of the phenomena predicted by the theoretical models of Kalmus and Maynard Smith (1966) and Seiger (1967). Further study would certainly reveal more information. Firstly, although it is inferred from our data, it certainly needs to be confirmed that it is the male who plays the dominant role in mate selection. Secondly, it is important to know whether a gosling becomes imprinted to either parent or simply to the mother. Thirdly, does the appearance of other goslings in the brood influence the imprinting? Fourthly, how absolute is the imprinting? Seiger showed that if imprinting was absolute and involving both sexes then sympatric speciation would take place within a few generations, even when the morphs differed by a single allele. Since Blue Geese and Snow Geese have been known to interbreed for more than 60 years (Blaauw, 1908), and since all types of mating are still known to occur it suggests that imprinting is less than absolute. The facts that the Blue Goose and the Lesser Snow Goose may differ by a single gene and that imprinting most probably has played a role in the distribution of the color genes in the population support the idea that imprinting, if absolute, could be a speciation mechanism.

Since the mechanism does not appear to be absolute, the assortative mating could well be a mechanism for maintaining the polymorphism in the population, without heterosis. The data presented above supports the conclusion that *A. caerulescens caerulescens* is polymorphic and consists of two color phases differing by a single major gene.

Summary

An analysis of a population of *Anser caerulescens* has led to an understanding of the genetic mechanisms involved in the polymorphism found in this group.

Basically, the polymorphism appears to be determined by a single pair of alleles, such that blue birds have the genotype BB or Bb whereas white birds have the genotype bb.

This simple interpretation is complicated by three factors. Firstly, dominance appears to be incomplete in most blue birds and a variable amount of white plumage on the belly occurs in most heterozygotes. Some of the homozygotes also have white plumage on the belly, and it is not possible to assign the genotype BB or Bb to a blue bird on the basis of plumage alone. A dark bellied blue bird is usually homozygous, a bird with much white on the belly is usually heterozygous. Secondly, there are variations in plumage which are not due to this major gene for polymorphism. This variation has been shown to have both genetic and nongenetic components. Thirdly, there is assortative mating.

The assortative mating has been examined in detail and a theory to explain it has been put forward. Basically, this theory postulates that males of this polymorphic species select mates which have plumage patterns similar to those of one of their parents. Some behavioral characteristic whereby the gosling becomes "imprinted" to the plumage of one of its parents could account for this mate preference and for the assortative mating which has been observed. This type of assortative mating may be the mechanism whereby the polymorphism is maintained in the population.

Since imprinting mechanisms are well known in geese and since the Blue-Snow goose complex is the only goose species with such pronounced plumage polymorphism, apart from the South American *Chloephaga picta*, it would seem to be an ideal species for a combined genetical and behavioral study, which could shed light on mechanisms of evolution dependent upon learned behavior.

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